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The relative densities and overlap zones of Fringilla cinctus (northern) and F. cristatus (southern), and of Fringilla montifringilla (northern) and F. coelebs (southern) were studied in censuses made in Finland in 1910-29, 1936-49, 1952-63 and 1973-77. The population changes of the species are described. F. cinctus greatly decreased, first in the southern and later in the middle parts of its range. F. cristatus first expanded both northwards and to the Åland Islands, but then decreased, particularly in the north. In their overlap zone, both species decreased drastically (by 90-95 %). F. montifringilla was stable, excepting a temporary decrease in the 1940's. F. coelebs increased, but the 1:1 zone of the Fringilla species has fluctuated mainly owing to fluctuations in the numbers and range of F. montifringilla.

Two major theories purport to account for the dynamics of North European biota: either the climatic amelioration of the past 100 yr is of importance, or recent habitat changes (often due to man or his livestock) are more effective. Recent changes in climate and habitat are correlated with population changes in order to test the two biogeographic theories. Climatic amelioration may account for some, but certainly not all population changes. Habitat changes (including the abandonment of forest grazing, the increase of spruce, increased edge effect, and extensive clear-cuttings particularly in N Finland) may explain most changes. A few short-term population changes were probably due to exceptional winter or spring weather.

The presumed interspecific competition between the congeners studied is examined critically. Standard competition equations do not adequately model the dynamics of the species pairs, but at least three additional points must be taken into account: environmental changes, population changes in relation to ecological saturation, and the evolutionary time scale.

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Climatic changes, habitat changes, and competition – dynamics of geographical overlap in two pairs of congeneric bird species in Finland

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The relative densities and overlap zones of Parus cinctus (northern) and P. cristatus (southern), and of Fringilla montifringilla (northern) and F. coelebs (southern) were studied in censuses made in Finland in 1910-29, 1936-49, 1952-63 and 1973-77. The population changes of the species are described. P. cinctus greatly decreased, first in the southern and later in the middle parts of its range. P. cristatus first expanded both northwards and to the Åland Islands, but then decreased, particularly in the north. In their overlap zone, both species decreased drastically (by 90-95 %). F. montifringilla was stable, excepting a temporary decrease in the 1940's. F. coelebs increased, but the 1:1 zone of the Fringilla species has fluctuated mainly owing to fluctuations in the numbers and range of F. montifringilla.

Two major theories purport to account for the dynamics of North European biota: either the climatic amelioration of the past 100 yr is of major importance, or recent habitat changes (often due to man or his livestock) are more effective. Recent changes in climate and habitats are compared with bird population changes in order to test the two biogeographic theories. Climatic amelioration may account for some, but certainly not all population changes. Habitat changes (including the abandonment of forest grazing, the increase of spruce, increased edge effect, and extensive clear-cuttings particularly in N Finland) may explain all long-term trends. A few short-term population changes were probably due to exceptional winter or spring weather.

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1. Introduction

us are close competitors. Their basic ecology has been described in standard handbooks, such as von Haartman et al. (1963-72), von Haartman (1969) or Lack (1971; Parus:30, 39, Fringilla: 89-91). In brief, P. cristatus breeds in coniferous forest, while P. cinctus also occurs in mixed forest. The feeding stations (Nilsson and Alerstam 1976) are similar, but the beak of P. cristatus is thinner. P. cristatus also breeds very early. Significant negative interaction between the two tits was suggested by Lack (1971:39), for he pointed out that P. cristatus is absent from Asia, and there P. cinctus reaches the southern border of the taiga.

Fringilla coelebs is a real habitat generalist among the Finnish forest birds (von Haartman 1969). F. montifringilla mainly breeds in sparse forest, including wooded bogs. The diets are similar, as well as the measurements. Merikallio (1951; see also Bergman 1952) suggests that there is interspecific territoriality between the Fringilla species, but the extensive unpublished data of A. Mikkonen (pers.comm.) from the main overlap zone of the species show great overlap of territories. The Fringilla species migrate to Central Europe, but the Parus species are sedentary.

It should be noticed that Merikallio (1951) did not regard the two Parus species as a fully satisfactory pair for his comparison, but he pointed out that the Parus genus and Regulus regulus might be a more proper unit, as they "seem to form biologically a single feeding unit". He was thus a forerunner of the modern concept of (feeding) guild (Root 1967), but the conclusions drawn below are valid also if the whole guild is analysed (for relevamt data, see Järvinen et al. 1977, Järvinen and Väisänen 1977a, 1979a).

2. Material and methods

The data were gathered using the line transect method (e.g. Järvinen and Väisänen 1976) in the breeding season, and they were analysed as explained in Järvinen and Väisänen 1977b. The

for 1936-77 was 142 observations on P. cinctus, 798 observations on P. cristatus, 6479 observations on F. montifringilla and 23 708 observations on F. coelebs. As the censuses were divided into three periods (1936-49, 1952-63, 1973-77), of which 1973-77 comprised almost 3/4, our statements on P. cinctus are based on tens of observations in each period, but there were hundreds (P. cristatus) or thousands (Fringilla spp.) of observations in the other species. The censuses had a fairly even distribution over the whole of Finland in each period (e.g. Järvinen and Väisänen 1979b).

In addition to our own data, we used those published by Merikallio (1951) in a similar study. His methods (Merikallio 1943) of 1910-29 were quantitative and he aimed at a representative coverage of different habitats. For the present purpose even the oldest data are thus applicable, as even a fairly crude method is adequate for establishing the relative proportions of the two Parus or the two Fringilla species, as the species compared are relatively similar with respect to censusing.

3. Recent climatic changes in Finland

Our strategy is first to describe recent changes in climate (this section), habitats (Sect. 4) and bird populations (Sect. 5), and then collate the facts in Sect. 6. We shall focus on Finland, but many trends have presumably been significant also elsewhere in northern Europe. Our climatic review is largely an ecological distillation of Heino (1978a, 1978b).

3.1. Long-term changes

Heino (1978a, 1978b) has summarized the change of the annual average temperature in Helsinki as follows. From about the 1870's to the 1930's, the average temperature increased by about 1.5°. In the 1950's, average temperature started to decline, but, owing

to the mild winters of the 1970's, temperature again increased about to the level of the 1930's and 1940's. Summer temperature changed relatively less than winter temperature; only the warm summers of the 1930's resulted in an average increase of 1°, and the averages have remained on this level since then. The amelioration of the northern regional climate, which started in the 19th century, was most pronounced in spring temperature, which increased by about 2° by the 1930's.

The long-term changes can also be mapped, for isotherms are displaced northwards as the climate ameliorates. As to April, the changes are largely negligible (von Haartman 1973). May isotherms (Fig. 1) migrated 100-200 km northwards from 1901-30 to 1931-60, but showed little changes in 1961-75, but June has become continuously warmer (Fig. 1); isotherms have moved as much as 300-400 km northwards at some places from 1901-30 to 1961-75. A similar change from 1901-30 to 1931-60 is shown by July isotherms (Hustich 1978), but the isotherms show a reversal of the ameliorating trend in 1961-75 (our unpublished data).

No weather indices were computed for our study periods, as annual variation is great compared with long-term trends: the standard deviation of monthly averages in temperature is 1-2 °C, in winter even 4°C (Kolkki 1966, 1969), but long-term trends rarely exceed 1°C. In consequence, brief exceptional periods affect any indices greatly. For example, an index for 1973-77 should certainly include the years 1971-75, but these were very warm years (since 1829, another five-year period, 1934-38, has been equally warm in Helsinki). But should we also include the late 1960's, when the winter temperatures averaged 3-4° less than the long-term (1931-60) average ?

3.2. Exceptional years

Winter temperatures has a great effect on winter mortality of

sedentary birds (e.g. Parus) or of those migrating to Central Europe (e.g. Fringilla). The severity of the winter in a wide region is indicated by the extent of ice cover in the Baltic; data are available since the winter of 1720 (=1719/20) (Jurva 1952, Palosuo 1965; later data from Merentutkimuslaitos, Helsinki). Following the classification by Palosuo, severe winters (ice cover more than 300 000 km^2) comprised (Fig. 2) 19 % of the winters in our study period (the long-term average for 1720-1950 was 30 %). Mild winters (ice cover less than 180 000 km^2) were frequent, 25 = 60 % (only 38 % in 1720-1950). Of great importance is the mild period since 1970; in fact, 1971-75 was the mildest five-winter period ever observed at weather stations in Helsinki! The winters of 1971-75 were also mild in Central Europe.

Exceptional years with regard to temperature during spring migration or breeding were defined on the basis of average temperature in April, May, June and July, using also the standard deviations of average temperature for 1931-60 (Kolkki 1966; for Sodankylä, our own data). We defined a monthly average as normal, if it did not belong to the 10 % tails of a normal distribution constructed from the average and standard deviation. The calculations have been summarized in Fig. 2. We observed 20.4 % exceptional months (expected 20 %), and cold and warm months were equally frequent (49 and 55, respectively). There were many warm months of June and cold months of July.

We conclude (Fig. 2) that effects of exceptional weather may be expected on our results in the 1950's owing to the cold spring of 1955 (39 % of the transects for 1952-63 were censused in 1955, and this percentage is much higher for N Finland) and in the 1970's owing to the preceding mild winters. Of course, monthly averages may be misleading, for warm and cold periods may occur within a month .

4. Recent habitat changes in Finland

As the species pairs studied by us breed in forests, we restrict our attention to changes in the structure of the Finnish forests. (For more comprehensive accounts of habitat changes, see von Haartman 1973, 1975). We follow Järvinen et al. (1977), whose data mainly come from the third (1951-53) and the sixth (1971-76) Finnish forest inventories.

1. The age structure of the forests has changed (Tab. 1). Clear-cuttings have been extensive, and young stands have thus become more common. As the areas cut are often small plots, especially in S Finland, the amount of edges has considerably increased. On the other hand, the area of old (over 140 yr) forests decreased by about 3500 km^2 from 1951-53 to 1971-76. Of great importance is probably the elimination of old/sick trees by foresters and the decreased average size of old forest areas. The cuttings of old forests were particularly extensive in N Finland in the late 1950's and early 1960's (Järvinen et al. 1977, especially their Fig. 2).

2. The proportion of spruce has greatly increased in S Finland (the recent trend in N Finland is different, but spruce is less important in the north). The percentage of spruce was 28 in S Finland in 1921-24, but it is now 42 (1971-76); this is an increase of 50 %. As forest areas have increased and the volume of the growing stock has increased, the absolute increase is even greater.

3. Peatland areas have been drained for forestry (40000 km^2, especially in the 1960's). Many of the areas drained grow young pine, but the birch Betula pubescens is also often dominant.

4. Artificial fertilization of forest areas started in the 1960's and about 20000 km^2 have now been fertilized. As a result, the herb and bush layers of the forests have become denser. A similar, but probably more important effect is due to two trends in agriculture: afforestation of agricultural areas and abandonment

of forest grazing by cattle. Both trends have created about 5000 km^2 forest areas, where deciduous bushes and young trees are abundant. Forest grazing was previously extensive (e.g. von Haartman 1973, his Fig. 11), and the forests not used for grazing were probably barren. Forest grazing disappeared gradually. According to von Haartman, it had decreased strongly in S and SW Finland in 1920, but in other parts of the country it was still common. As late as 1938, more than 65000 km^2 of forests were still used for grazing. The effect of forest grazing is profound: wood production may decrease 50 % (Romell, ref. von Haartman 1973), the rejuvenation of deciduous trees is difficult and young spruce are badly damaged.(e.g. Lampimäki 1939). Forest grazing has certainly greatly affected Finnish bird populations (von Haartman 1973, Haila et al. 1980).

5. Dynamics of the species pairs

For the purposes of the present paper, many details of the census results are irrelevant. Therefore, we shall summarize our data, to be published later in book form. The densities and frequencies (%) of the four species studied are shown in Fig. 3. As the 1:1 zones given by Merikallio (1951) are based on the numbers of observations and not on densities, his zones are directly comparable with our zones (1973-77) only if the zone for Parus is displaced slightly southwards and that for Fringilla slightly northwards (see Järvinen and Väisänen 1977b). In effect, the displacement would have been so small that it was not made at all, especially because the conclusions are identical. Another point is that Merikallio (1951) gives his period as 1910-29. Actually, it was probably 1915-29 (cf. Merikallio 1943). (Curiously enough, the period was given as 1910-21 for Fringilla, but this was probably a misprint.)

5.1. Parus

Densities. At present, maximum densities of P. cinctus occur in Forest Lapland (0.5 to 1 p km^{-2}, or pairs/km^2) and those of P. cristatus in S Finland (over 4 p km^{-2}), see Fig. 4A. There is an about 300 km broad zone where the two species overlap, but neither of them reaches the density of 0.25 p km^{-2} (a small area in N Finland being an exception, probably owing to chance).

In recent decades, P. cristatus has increased and P. cinctus has receded in N Finland (Merikallio 1951, 1958, von Haartman et al. 1963-72), but the trend since the 1940's is different (Järvinen and Väisänen 1977a, 1979a): both species have decreased, P. cristatus by about 50 % and P. cinctus by about 80 % since the 1940's. In the overlap zone of the two species, the changes have been drastic: P. cinctus had densities of about 5 p km^{-2} in zones 74-75 in the 1940's, while the present densities are 0.2 to 0.4 p km^{-2} (decrease 90-95 %); P. cristatus had densities of 1 to 2 p km^{-2} in zones 72-73 in the 1940's and 1950's, but the present density is about 0.1 p km^{-2} (decrease 90-95 %). The northernmost populations of P. cristatus and the southernmost populations of P. cinctus have decreased probably at least as drastically, though the data are too scanty for computations. The decrease of P. cristatus mainly occurred since the 1950's, but - as almost all censuses made in the main range of P. cinctus were made in 1955 - it is difficult to date exactly the decrease of P. cinctus.

The 1:1 zone. The 1:1 zone has shifted 100-200 km northwards from 1910-29 to the 1970's (Fig. 4B); owing to paucity of data, the change from the 1940's to the 1970's is not reliable.

5.2. Fringilla

Densities. At present, maximum densities of F. montifringilla are about 16 p km^{-2} (Forest Lapland) and those of F. coelebs exceed 50 p km^{-2} (S Finland). As the species are among the most common Finnish land birds, a more detailed map of their ratios could be drawn (Fig. 5A). The gradient is extremely steep - the ratio of the densities shows a 10000-fold change within about 600 km!

Merikallio (1951) suggested that F. montifringilla decreased by about a half from 1910-29 to 1941-49, while F. coelebs increased slightly. His calculations were based on the assumption that the total numbers of Fringilla spp. were constant (7050000 pairs). As two different sets of data from S Finland (Järvinen and Väisänen 1978, Haila et al. 1980) suggest a substantial increase of F. coelebs from the 1920's and 1930's to the 1940's (and 1970's), we reanalysed Merikallio's data assuming that the change observed in S Finland is valid for the whole population. However, the reanalysis confirmed Merikallio's suggestion; F. montifringilla was, as far as can be judged, about as abundant in 1910-29, 1952-63 and 1973-77.

The trend in F. coelebs is different. The increase from the 1920's and 1930's to the 1940's was substantial, but slight since then.

The 1:1 zone. The cold spring of 1955 is reflected in our results for F. montifringilla: the Finnish population seems to have bred, on average, 100-200 km more to the south than normally. So the 1:1 zone was also much more southern than the present one. A southern 1:1 zone was also observed by Merikallio (1951) in 1910-29, but it was northern in 1941-49 (Fig. 5B).

6. Discussion

6.1. Changes of climate and habitats as biogeographic agents

Merikallio (1951) interpreted the changes in the geographical

overlap in Parus and Fringilla on the basis of climatic trends. von Haartman (1973:454) discussed this interpretation, pointing out that, "Whether the cause is the climate...or habitat changes is difficult to judge". For Fringilla, von Haartman gives some data indicating that habitat changes may be important, but definite conclusions are not drawn. The two species pairs thus still provide major evidence for the theory that the climatic amelioration during the past 100 yr has been a biogeographic agent of importance.

Above, we have given data on bird population changes and changes of climate and habitats. The evidence has been collated in Tab. 2. The following additional comments refer to this table.

1. The impact of forestry here refers mainly to extensive clear-cuttings in N Finland.

2. The long-term increase refers to the first half of this century. The spruce hypothesis is due to von Haartman (1973).

3. No data given here, but the colonization has been documented by Palmgren (1927) and von Haartman (1963). Because spruce was increasing already during the colonization, the numbers attempting colonization may have been increased, and the climatic amelioration may have acted in the same direction (von Haartman 1963). As colonization always includes stochastic components, chance cannot be excluded, either.

6. We do not see plausible mechanisms explaining a drastic reduction of breeding numbers after a cold spring, and we therefore doubt it. Population fluctuations are an ad hoc explanation, and we therefore do not invoke it. However, because cold spring delays breeding (Slagsvold 1977), a methodological error due to the cold spring of 1955 may have been introduced here; in any case, the breeding of Carduelis flammea in 1955 was delayed in Lapland about two weeks, perhaps even more (von Haartman 1969).

The second half of May is the probable peak of laying in P. cinctus (von Haartman 1969), and the incubation period lasts about 17 days (A. Järvinen 1978). It seems thus probable that the latter half of June, the most important censusing period in N Finland, coincided with incubation of P. cinctus in 1955 (but not in the 1940's or the 1970's). If so, the drastic decrease of P. cinctus before 1955 was merely apparent. This is supported by Silvola's data in Hildén (1968) from northernmost Finland: the density in 1955 was normal, though the samples were very small (1-9 pairs). In our opinion, the most probable explanation is that there was a methodological error due to the early phenological time of the censuses in N Finland in the 1950's.

7. The breeding territory of P. cinctus seems to be very large compared with other tits (Haftorn 1973), which may play a role here.

10. Southern breeding occurs commonly after cold springs (von Haartman et al. 1963-72).

11. The favourable effect of spruce on F. coelebs was documented by Engström (1955). von Haartman (1969) stresses the importance of forests of high grade, and their coverage has certainly increased after the abandonment of forest grazing (cf. Haila et al. 1980). Forestry practices have also changed. The economically valuable trees were previously often cut, and the forest remaining comprised younger trees in sparse stands, which are poor for both birds and forestry. Improvements of forestry were certainly caused by the Private Forest Act of 1928. We are not able to order the causes connected with changes of forest structure, especially because F. coelebs is a habitat generalist (except in its northern margin), but they seem to us a more probable cause than climatic amelioration. However, the substantial early increase of the population might partially be due to decreased winter mortality owing to amelioration, and a completely unknown factor is hunting, which has probably decreased in the wintering area of F. coelebs.

We thus conclude that the effects of forestry have certainly had profound long-term effects on the two species pairs studied here. The theory that the changes observed are mainly regulated by climate is partially refuted. The only points in Tab. 2 which cannot be explained by habitat changes are 6 (probably a methodological problem) and 9-10 (temporary population changes probably related to exceptional weather). So short-term climatic effects must be invoked, but the role of long-term climatic changes is not clear. The technique developed by von Haartman (1973) based on mapping isotherms of different periods (see Fig. 1) suggests that some effects may have been profound. The main difficulty is that "climatic amelioration" is a vague term, and causal mechanisms relating climatic changes with basic population parameters are seldom specified.

The decrease of P. cinctus has usually been attributed to amelioration. The only plausible causal mechanism seems to be to invoke P. cristatus or some other southern competitor. It is now clear that this solution does not work, and the drastic decrease must mainly be due to habitat changes. This standpoint is supported by the fact that A. Järvinen (1978) attributes the poor breeding success in a northern population of P. cinctus to "adverse climate". However, we do not completely dismiss possible effects of competitors (though they may have been increased due to habitat changes, not necessarily owing to amelioration). So Phylloscopus trochilus, a dominant summer visitor, may be an effective competitor against Parus spp. (Ulfstrand 1976), and, according to our unpublished transect data, the population has increased in N Finland in recent decades.

Hildén (1968) studied the invasion of P. cinctus in Finland in 1963-64, and he suggested that such invasions may also have

occurred previously, but they have not been observed by the few ornithologists of earlier times. While probably sound, this suggestion may be only a partial explanation, especially because the southern populations of P. cinctus were earlier much denser. Our data support the hypothesis that the invasion of 1963-64 was particularly intense, compared with earlier invasions, because modern forestry has greatly decreased the coverage of mature forests in N Finland; extensive cuttings started in N Finland in the 1950's. So the threshold of population density leading to invasion (see Hildén 1968) may have decreased substantially. As to the invasion of 1963-64, we point out that the tits had experienced a particularly warm spring just before breeding (both April and May were exceptionally warm in Sodankylä in 1963, Fig. 2). Because the tit numbers were high before the invasion of 1963 (Hildén 1968), the climatic theory receives an additional blow.

6.2. Interspecific competition

The complementary distribution maps of the species compared (Voous 1960, Haftorn 1971) strongly suggest that interspecific competition is an important biogeographic factor, if not in an ecological time scale, so in an evolutionary perspective (see also Lack 1971). Competition on a geographical gradient presents interesting problems (Pielou 1975), but our data indicate that the problems may be more complex than generally realized.

First, competition is usually modelled using equations predicting compensatory population changes of the competitors. This prediction is not valid in the two cases studied here, as habitat trends are (and climatic trends may be) over riding. MacArthur (1972) predicted, on theoretical grounds, that a gap may exist between two competitors if the area between their main

ranges is too unproductive. It seems that intensive forestry in N Finland has almost succeeded in providing a verifying instance of MacArthur's theory, for the two Parus species are very rare in their present overlap zone! The overlap of the Fringilla species has fluctuated, but not as the competition theory proposes: the fluctuations have not been due to compensatory population changes, but fluctuations in F. montifringilla.

Second, Wiens (1977) emphasized that populations may experience "ecological crunches" in variable climates; such crunches nullify the assumptions of the competition theory and limit the usefulness of short-term studies. He stresses the importance of long-term studies in exploring alternative and complementary processes which should also be considered in addition to competition (not: instead of competition). Finnish line transects seem very useful on this point, and the present results contrast sharply with those of Merikallio (1951): on the basis of pure-bred competition theory, he suggested that the dynamics of the two species pairs can be understood as a result of climatic changes affecting the balance of two competitors (or, in Parus, the balance of a feeding guild). Certainly, the present view that habitat changes have been a factor of great importance does not rule out competition (particularly diffuse competition), for we have not studied the causal mechanisms relating habitat changes with changes in population parameters. Interspecific competition may be important in such mechanisms.

Third, we raise the question of the time scale. Assuming that short-term competitive effects are important is equivalent to assuming that populations tend to be near to their "saturated" levels, but this is a hazardous assumption (Wiens 1977, O. Järvinen 1978), especially in N Scandinavia with unstable bird populations (O. Järvinen 1979). The best evidence for the existence of significant interspecific competition in the species studied

seems to be the complementarity of their ranges; but this may be an evolutionary rather than an ecological effect, though drawing a sharp boundary between the two time scales is doubtful.

We conclude that the species pairs studied by us in this paper cannot be adequately understood if they are modelled using standard competition equations. At least three additional points must be taken into account in successful models: environmental changes (affecting the carrying capacity of the populations), population changes owing to climatic variability, and the evolutionary time scale.

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References

Bergman, G. 1952. Revier und Verhalten eines ungepaarten Bergfinkenmännchens (Fringilla montifringilla L.). - Ornis Fennica 29: 105-107.

Bezzel, E. 1977. Verbreitungsmuster von Zwillingsarten am Nordrand der Bayerischen Alpen. - Verh. Orn. Ges. Bayern 23: 1-18.

Brinck, P. 1966. Djurvärlden och det nordiska landskapets utveckling. - Norsk entomologisk Tidsskrift 13: 205-244.

Cody, M. L. 1974. Competition and the structure of bird communities. - Princeton Univ. Press, Princeton, N. J.

Engström, K. 1955. The dependence of the bird fauna on the composition of the forest. - Medd. Statens Skogsforskningsinstitut 45 (2): 1-47 (in Swedish with English summary).

Haartman, L. von 1963. The crested tit on the Åland Islands. - Ornis Fennica 40: 12-20.

- 1969. The nesting habits of Finnish birds. I. Passeriformes. - Comment. Biol. Soc. Scient. Fennica 32: 1-187.

- 1973. Changes in the breeding bird fauna of North Europe. - In: Breeding biology of birds, National Acad. Sciences, Washington D. C., pp. 448-481.

- 1975. Changes in the breeding bird fauna of coastal bays in southwestern Finland. - Ornis Fennica 52: 57-67.

- 1978. Changes in the bird fauna in Finland and their causes. - Fennia 150: 25-32.

- , Hildén, O., Linkola, P., Suomalainen, P. and Tenovuo, R. 1963-72. Pohjolan linnut värikuvin I-II. - Otava, Helsinki.

Haftorn, S. 1971. Norges fugler. - Universitetsforlaget, Oslo.

- 1973: A study of the siberian tit Parus cinctus during the breeding season. - Sterna 12: 91-155 (in Norwegian with English summary).

Haila, Y., Järvinen, O. and Väisänen, R. A. 1980. Effects of changing forest structure on long-term trends in bird populations in SW Finland. - Ornis Scand. 11 (in press).

Heino, R. 1978a. Climatic changes in Finland during the last hundred years. - Fennia 150: 3-13.

- 1978b. On climatic changes in Finland. - Danish Meteorological Institute Climatological Papers 4: 68-75.

Hildén, O. 1968. Die Invasion der Lapplandmeise, Parus cinctus, in Finnland 1963/64. - Vogelwarte 24: 189-198.

Hustich, I. 1978. A change in attitudes regarding the importance of climatic fluctuations. - Fennia 150: 59-65.

Jurva, R. 1952. On the variations and changes of freezing in the Baltic during the last 120 years. - Fennia 75: 17-24.

Järvinen, A. 1978. Breeding biology of the siberian tit Parus cinctus in northern Lapland. - Ornis Fennica 55: 24-28.

Järvinen, O. 1978. Are northern bird communities saturated? - Anser, Suppl. 3: 112-116 (in Swedish with English summary).

- 1979. Geographical gradients of stability in European land bird communities. - Oecologia 38: 51-69.

- and Väisänen, R. A. 1976. Finnish line transect censuses. - Ornis Fennica 53: 115-118.

- and Väisänen, R. A. 1977a. Recent quantitative changes in the populations of Finnish land birds. - Polish Ecol. Studies 3(4): 177-188.

- and Väisänen, R. A. 1977b. Constants and formulae for analysing line transect data. - Mimeo., 10 pp., Helsinki.

- and Väisänen, R. A. 1978. Long-term population changes of the most abundant south Finnish forest birds during the past 50 years. - J. Orn. 119: 441-449.

- and Väisänen, R. A. 1979a. Changes in bird populations as criteria of environmental changes. - Holarctic Ecol. 2: (in press).

- and Väisänen, R. A. 1979b. Numbers of migrants and densities of breeding birds: a comparison of long-term trends in North Europe. - Anser 18: (in press) (in Swedish with English summary).

- , Kuusela, K. and Väisänen, R. A. 1977. Effects of modern forestry on the numbers of breeding birds in Finland in 1945-1975. - Silva Fennica 11: 284-294 (in Finnish with English summary).

Kalela, O. 1952. Changes in the geographic distribution of Finnish birds and mammals in relation to recent changes in climate. - Fennia 75: 38-51.

Keränen, J. 1952. Temperaturkarten von Finnland für den Zeitraum 1901-30. - Mitteilungen der Meteorologischen Zentralanstalt des finnischen Staates 36: 1-24.

Kolkki, O. 1966. Tables and maps of temperature in Finland during 1931-1960. - Meteorological Yearbook of Finland 65 (Suppl. 1a): 1-42.

- 1969. Katsaus Suomen ilmastoon. - Ilmatieteen Laitoksen Tiedonantoja 18: 1-64.

Lack, D. 1971. Ecological isolation in birds. - Blackwell Scientific Publications, Oxford and Edinburgh.

Lampimäki, T. 1939. Nautakarjan laiduntamisesta metsämailla. - Silva Fennica 50: 1-106.

MacArthur, R.H. 1972. Geographical ecology. - Harper & Row, New York.

Merikallio, E. 1943. Über die Taxierung der Vogelzahl in Finnland. - Ann. Zool. Soc. 'Vanamo' 9 (Notulae Zool.): 20-29. (in Finnish with Deutsch summary).

- 1951. Der Einfluss der letzten Wärmeperiode (1930-49) auf die Vogelfauna Nordfinnlands. - Proc. X Int. Ornithol. Congr. (Uppsala): 484-493.

- 1958. Finnish birds. Their distribution and numbers. - Fauna Fennica 5: 1-181.

Nilsson, S. G. and Alerstam, T. 1976. Resource division among birds in North Finnish coniferous forest in autumn. - Ornis Fennica 53: 15-27.

Palmgren, P. 1927. Die Haubenmeise (Parus cristatus L.) auf Åland. - Acta Soc. Fauna Flora Fennica 56: 1-12.

Palosuo, E. Duration of ice along the Finnish coast 1931-1960. - Merentutkimuslaitoksen Julkaisuja 219: 1-49.

Pielou, E.C. 1975. Ecological diversity. - John Wiley & Sons, New York, London, Sidney, Toronto.

Romell, L.-G. 1964. Skog och odling i svensk "natur". - Sveriges Nat. Årsbok 1964: 110-124.

Root, R.B. 1967. The niche exploitation pattern of the blue-grey gnatcatcher. - Ecology 52: 1065-1070.

Slagsvold, T. 1977. Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. - Ornis Scand. 8: 197-222.

Sylvén, M. 1978. Interspecific relations between sympatrically wintering common buzzards Buteo buteo and rough-legged buzzards Buteo lagopus. - Ornis Scand. 9: 197-206.

Ulfstrand, S. 1976. Feeding niches of some passerine birds in a South Swedish coniferous plantation in winter and summer. - Ornis Scand. 7: 21-27.

Voipio, P. 1956. The biological zonation of Finland as reflected in zootaxonomy. - Ann. Zool. Soc. 'Vanamo' 18 (3): 1-36.

Voous, K. H. 1960. Atlas of European birds. - Nelson, London.

Wallgren, H. 1954. Energy metabolism of two species of the genus Emberiza as correlated with distribution and migration. - Acta Zool. Fennica 84: 1-110.

Wiens, J. A. 1977. On competition and variable environments. - Amer. Scientist 65: 590-597.

Williamson, K. 1975. Birds and climatic change. - Bird Study 22: 143-164.

Tab. 1. Age structure of the Finnish forests in 1951-53 and 1971-76 (modified from Järvinen et al. 1977).

	1951-53		1971-76		Change
	1000 km^2	(%)	1000 km^2	(%)	1000 km^2
Treeless regeneration area	1.0	(1)	7.9	(4)	+ 6.9
Forest stands of 1-20 years	7.5	(4)	28.4	(14)	+ 20.9
" " 21-40 years	20.3	(12)	25.1	(13)	+ 4.8
" " 41-60 years	36.4	(21)	30.8	(16)	- 5.7
" " 61-80 years	34.0	(19)	35.9	(18)	+1.9
" " 81-100 years	24.0	(14)	24.3	(12)	+ 0.3
" " 101-120 years	15.1	(9)	14.8	(7)	- 0.3
" " 121-140 years	10.8	(6)	9.3	(5)	- 1.5
" " over 140 years	24.5	(14)	20.9	(11)	- 3.6
Total	173.6	(100)	197.3	(100)	+ 23.7

Tab. 2. The population changes observed and their suggested explanations. In the third column, C indicates that the climatic theory is supported, while H refers to the theory that habitat changes have been important. See text for comments.

Population changes	Suggested explanation	Theory supported
Parus		
1. Long-term decrease of cinctus	Climatic amelioration, or impact of forestry	C or H
2. Long-term increase of cristatus in N Finland	Climatic amelioration, or increase of spruce	C or H
3. Colonization of Åland by cristatus (and possible early increase in S Finland)	Increase of spruce, or chance; hardly climate	H
4. Recent drastic decrease of both cristatus and cinctus in the overlap zone of the species	Impact of forestry (since the 1950s); not climate	H
5. Less drastic recent decrease in northern populations of cinctus and in S Finnish populations of cristatus	Less intensive forestry than in the areas where the populations have catastrophically declined; increase of spruce in S Finland; hardly climate	H
6. Drastic decrease of cinctus from the 1940s to 1955	The very cold spring of 1955, or population fluctuations, or failure of census in 1955; not forestry	C?

(TABLE 2 continued)

7. Northward change of the 1:1 zone of the species from 1910-29 to 1973-77	Climatic amelioration, or greater negative impact of forestry on cinctus	C or H
Fringilla		
8. Long-term stability of montifringilla in Finland	Wide habitat amplitude in N Finland; not climate	H
9. Temporary decrease of montifringilla in the 1940s	Cold winters of the early 1940s, or population fluctuations; not forestry	C?
10. Southward shift of montifringilla in 1955	The very cold spring of 1955; not forestry	C
11. Long-term increase of coelebs in Finland	Climatic amelioration, or increase of edge effect, spruce and forests of high grade in S Finland, or decreased winter mortality	C or H
12. Changes of the 1:1 zone of the species	Temporary decrease of montifringilla in the 1940s (point 9) and southern breeding in 1955 (point 10)	-

Legends to figures

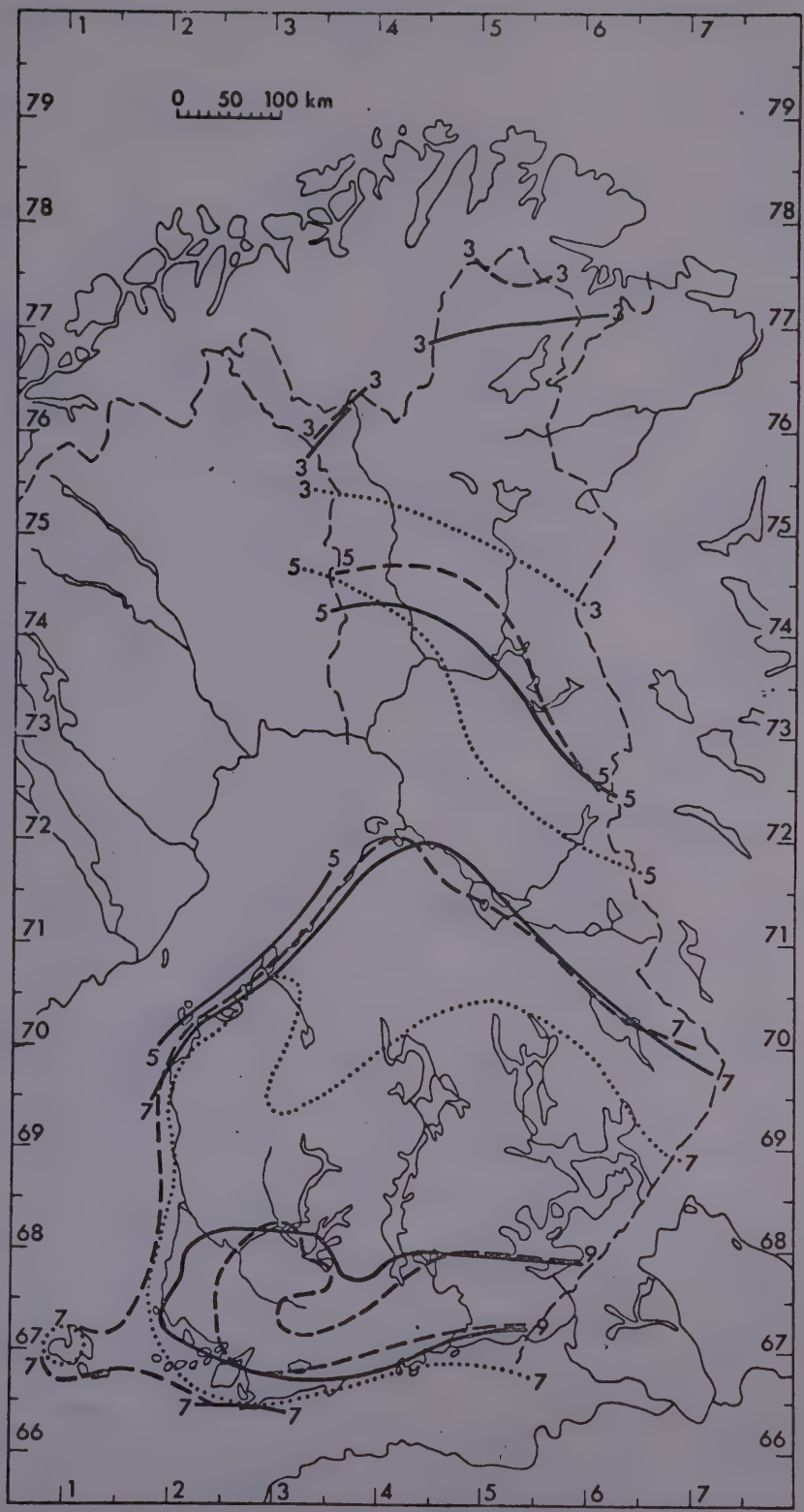
Fig. 1. May (left) and June (right) isotherms in 1901-30 (.....), 1931-60 (-----) and 1961-75 (——). (Keränen 1952, Kolkki 1966, unpubl. data of R. Heino for 1961-75.) The coordinates refer to the Finnish uniform grid.

Fig. 2. Exceptional years with regard to winter temperature and monthly average temperature in April - July in Finland in 1936-77. The severity of the winter is indicated by the extent of ice cover in the Baltic (= = very cold, - = cold; no symbol = intermediate "normal" winters; + = mild, ‡ = very mild). Monthly mean temperatures are from (H) Helsinki, (O) Oulu and (S) Sodankylä (- = cold, + = warm; the probability of their occurrence is once in 10 years or less, see text). The most important transect census years are shaded.

Fig. 3. Densities (pairs km^{-2}) and frequencies (in parenthesis) of the four species studied in 100-km zones of Finland in 1973-77.

Fig. 4. A. The densities of Parus cinctus and P. cristatus in 1973-77. Hatching = density 0.25-0.5 pairs km^{-2}, cross-hatching = density over 0.5 pairs km^{-2}. The 1:1 zone of the two species also shown; notice that this zone occurs in an area where both species are sparse, and the zone is thus quite unreliable. B. The 1:1 zones of the Parus species in three study periods. The two earlier periods are based on Merikallio (1951).

Fig. 5.A. The ratio of the densities of Fringilla montifringilla and F. coelebs in 1973-77. B. The 1:1 zones of the Fringilla species in three study periods. The two earlier periods are based on Merikallio (1951).



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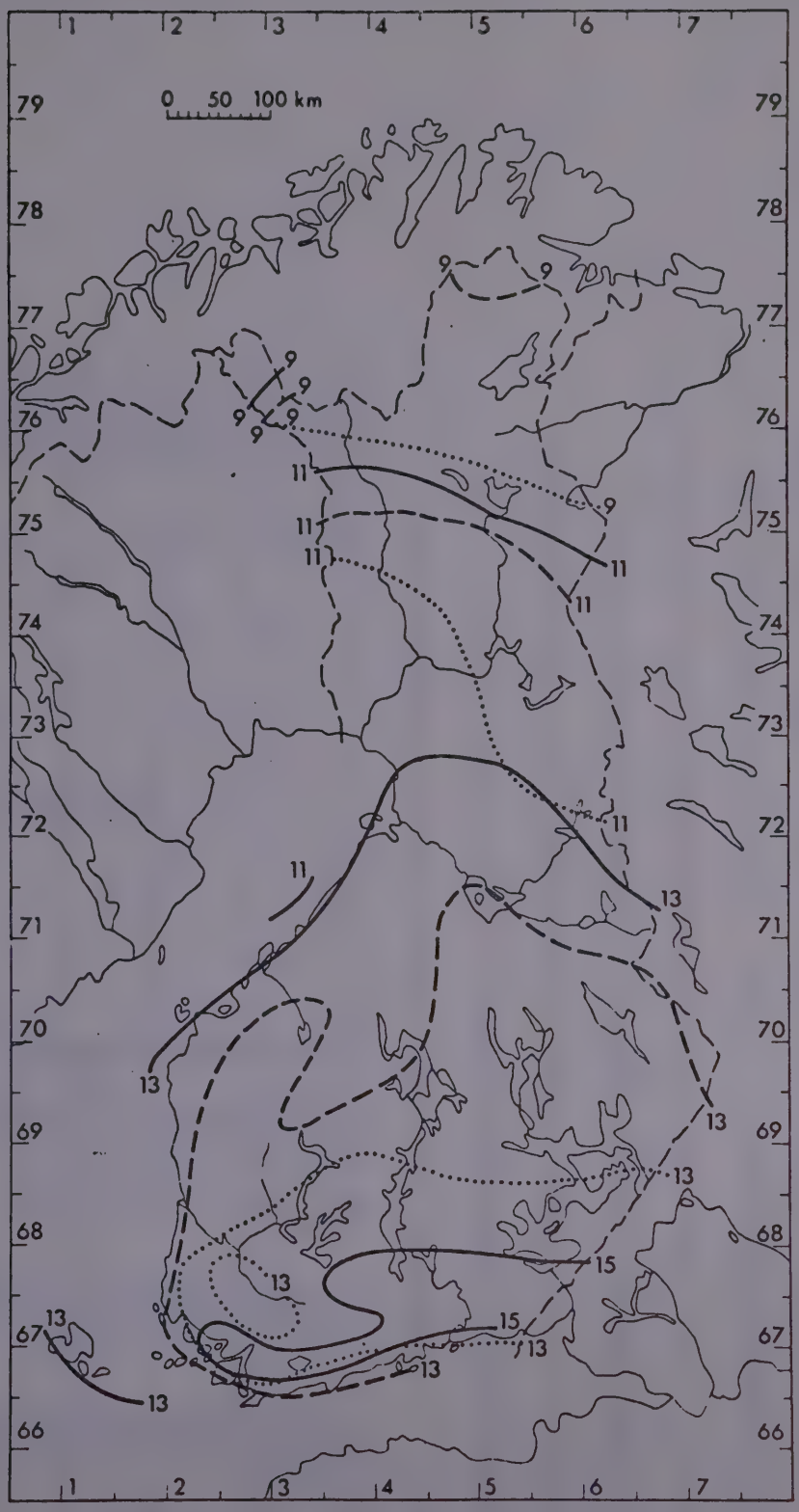

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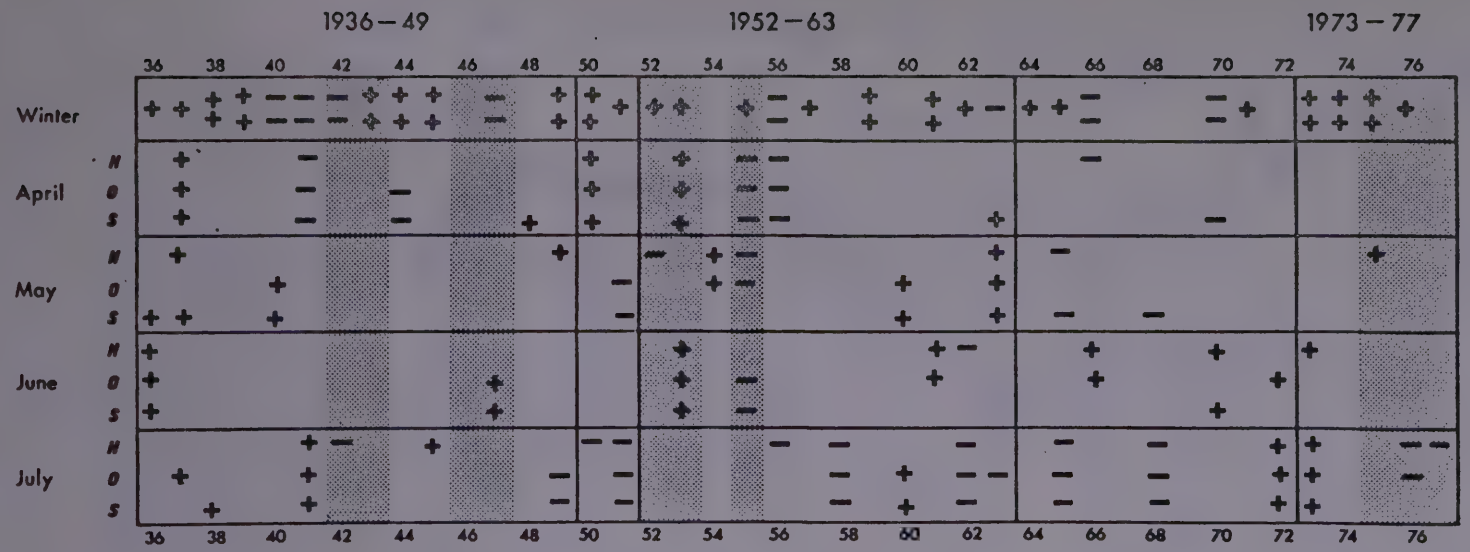

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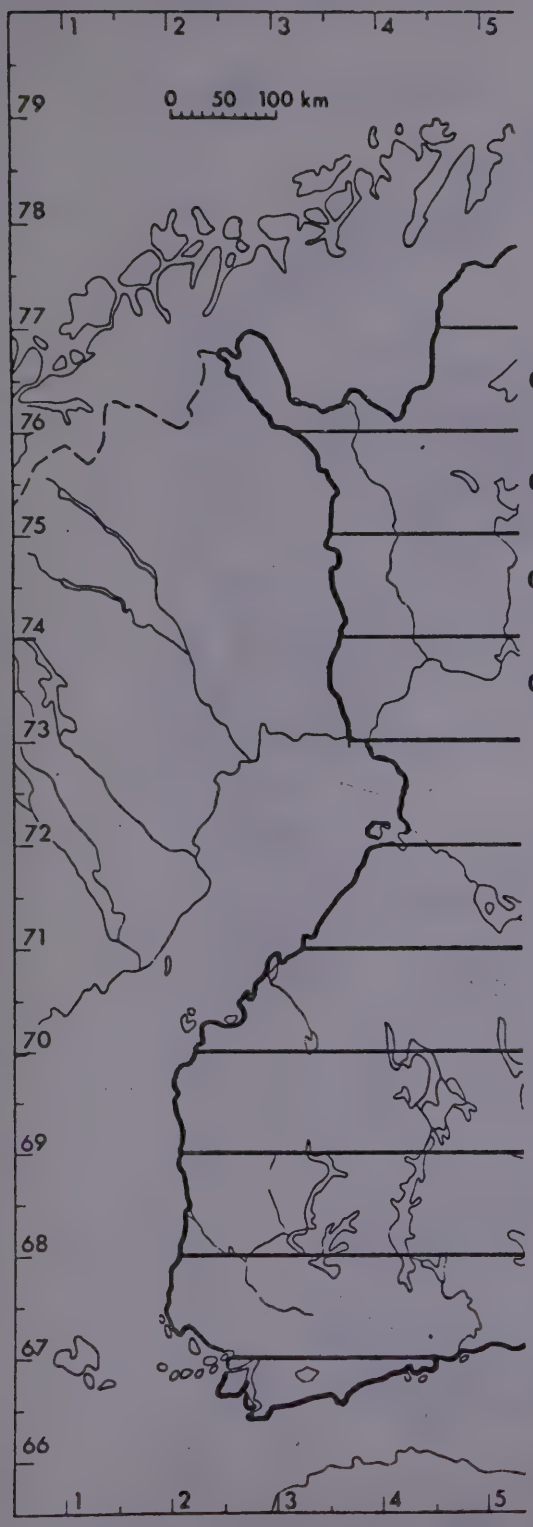


Parus cinctus	Parus cristatus	Fringilla montifringilla	Fringilla coelebs
—	—	6.8(9.5)	—
0.8(0.8)	—	12.3(12.9)	—
0.5(0.5)	—	15.8(17.3)	0.5(0.6)
0.2(0.2)	0.1(0.0)	11.9(10.3)	3.2(2.8)
0.1(0.0)	0.2(0.1)	9.5(8.6)	10.3(8.2)
—	0.0(0.0)	5.8(4.5)	13.7(10.7)
—	0.8(0.5)	2.7(1.8)	20.9(14.0)
—	1.7(0.8)	1.5(0.7)	37.0(17.8)
—	1.8(0.9)	1.1(0.6)	37.9(20.1)
—	2.1(0.8)	0.1(0.0)	47.6(19.1)
—	3.3(1.3)	0.0(0.0)	51.6(20.2)

Fig. 3. Densities (pairs km^{-2}) and frequencies (in parenthesis) of the four species studied in 100-km zones of Finland in 1973-77.

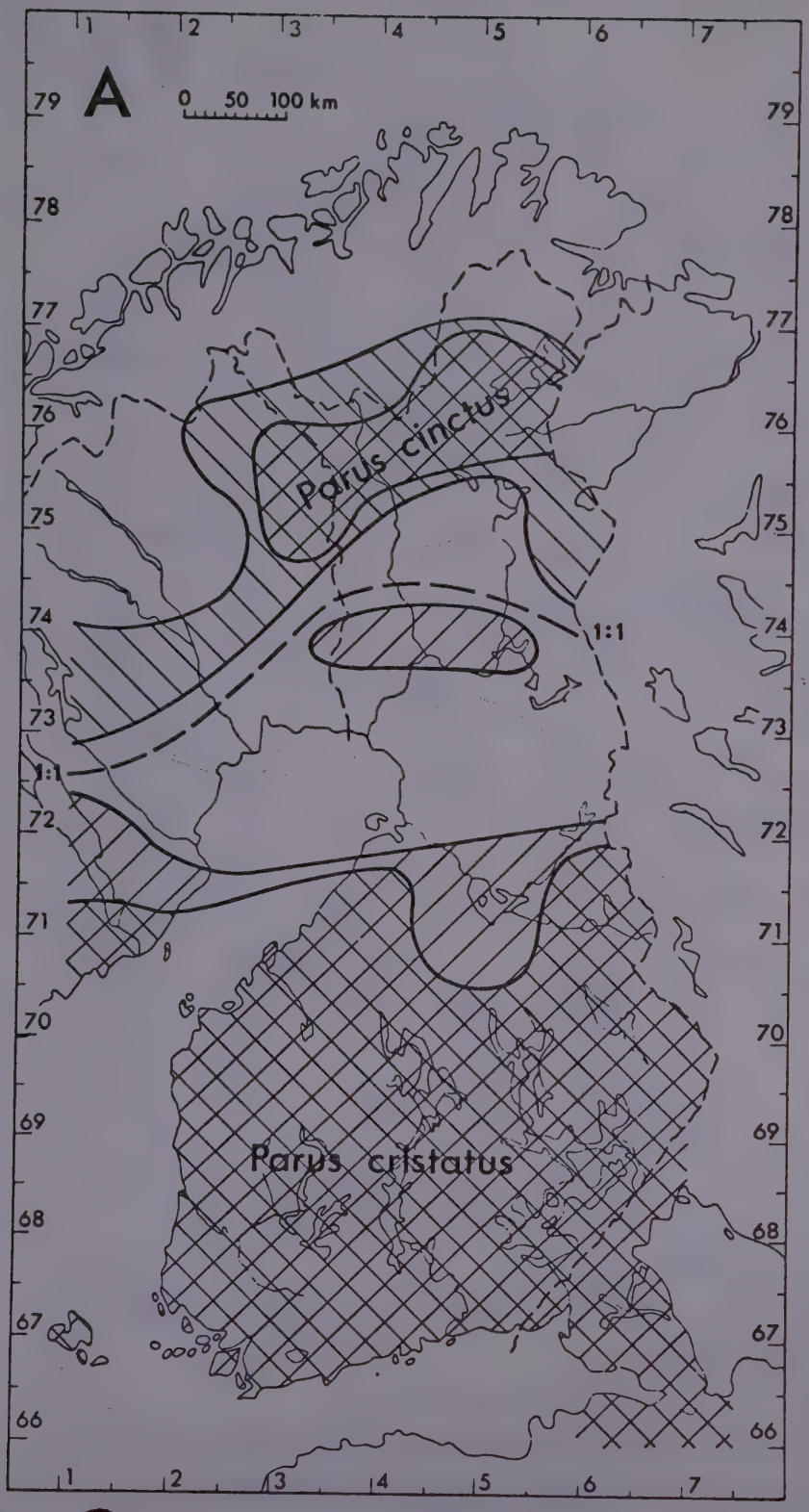
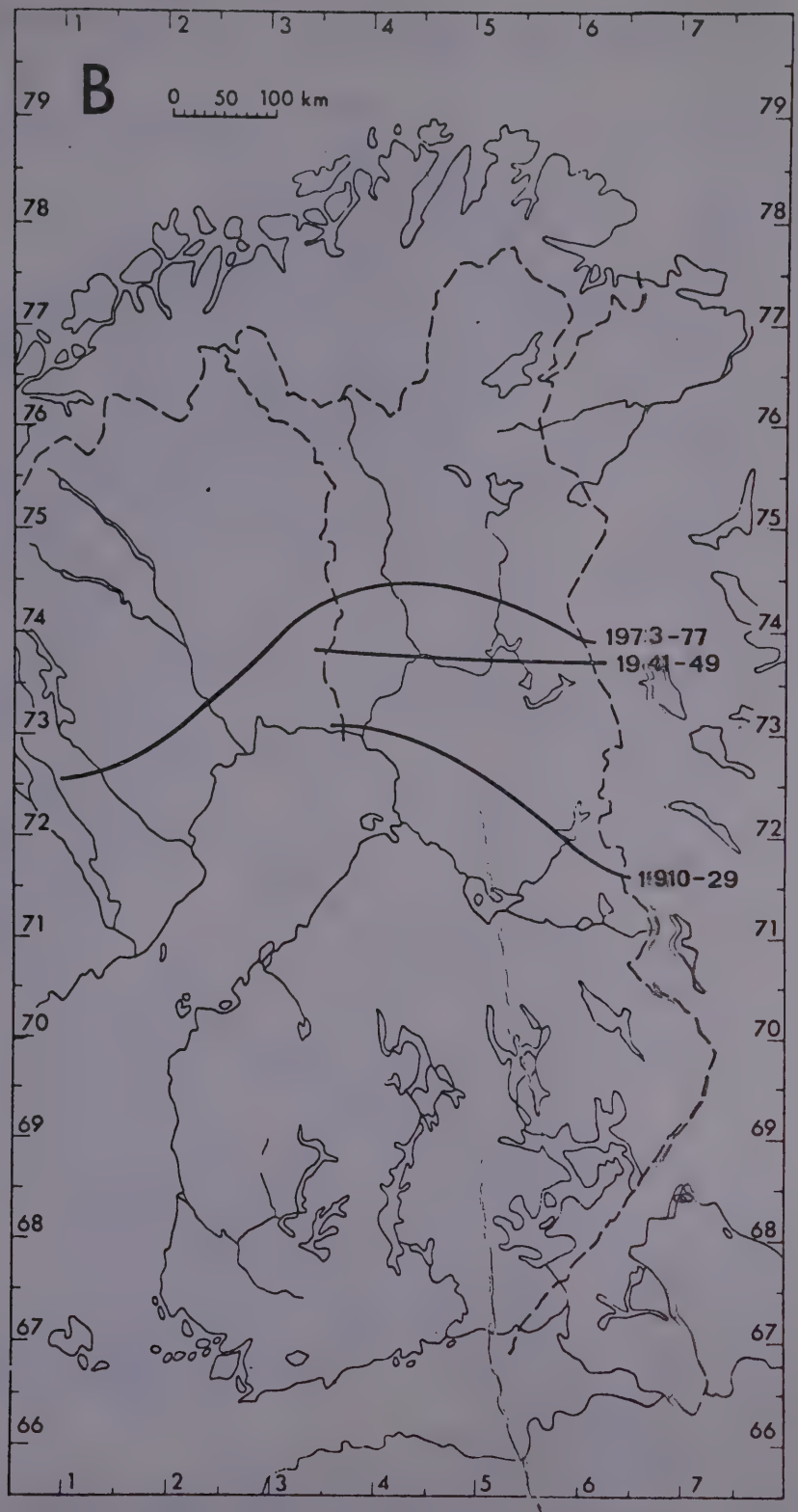


Fig. 4. (A.) The densities of Parus cinctus and P. cristatus in 1973-77. Hatching = density 0.25-0.5 pairs km^{-2}, cross-hatching = density over 0.5 pairs km^{-2}. The 1:1 zone of the two species also shown; notice that this zone occurs in an area where both species are sparse, and the zone is thus quite unreliable. B. The 1:1 zones of the Parus species in three study periods. The two earlier periods are based on M.erikallio



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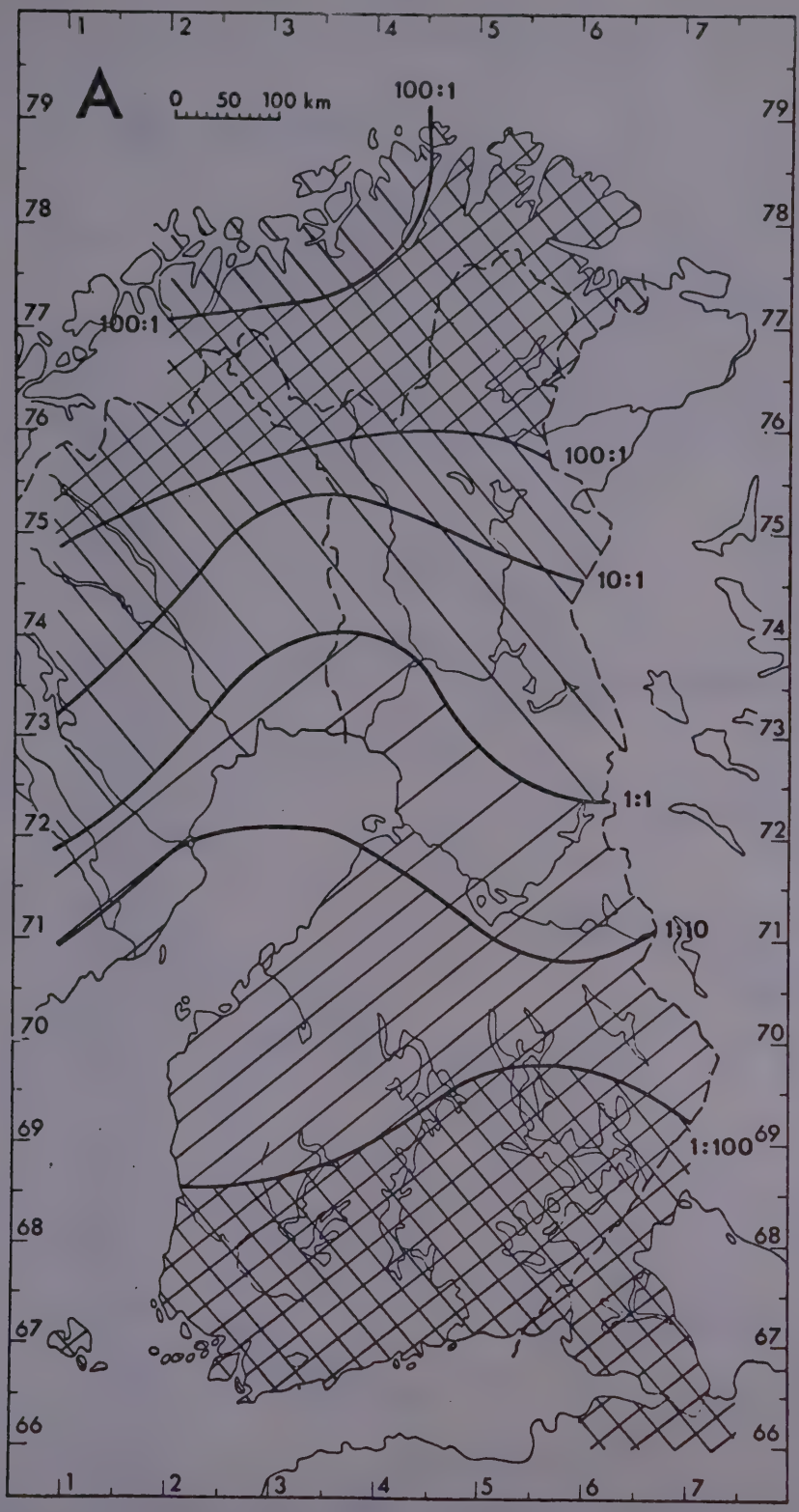

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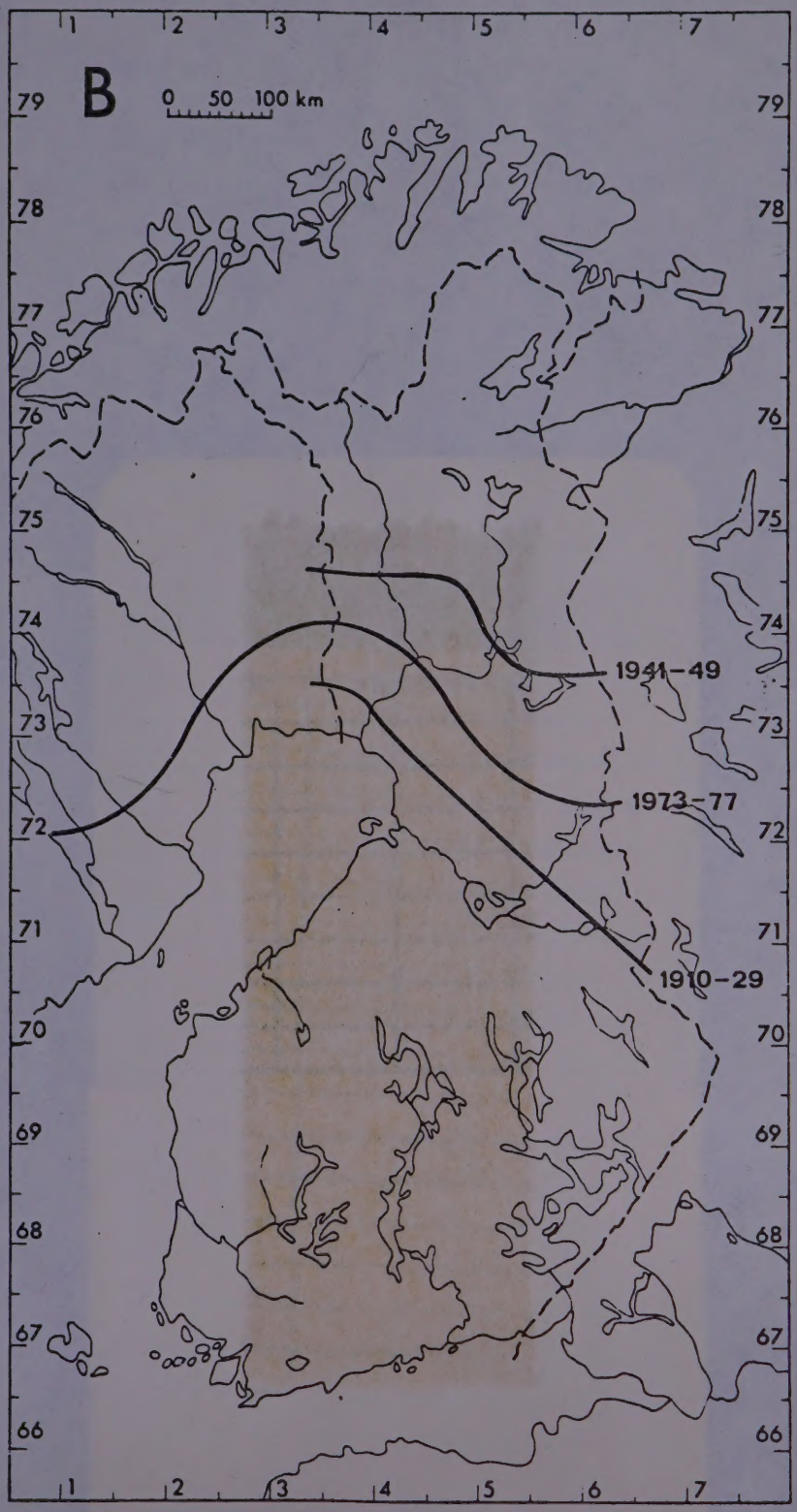

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